1904

U. S. DEPARTMENT OF AGRICULTURE.
BUREAU OF PLANT INDUSTRY—BULLETIN No. 63.
B. T. GALLOWAY, *Chief of Bureau.*

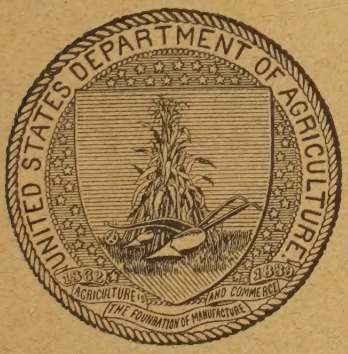
INVESTIGATIONS OF RUSTS.

BY

MARK ALFRED CARLETON,
CEREALIST IN CHARGE OF CEREAL INVESTIGATIONS.

VEGETABLE PATHOLOGICAL AND PHYSIOLOGICAL INVESTIGATIONS.

ISSUED JULY 12, 1904.



WASHINGTON:
GOVERNMENT PRINTING OFFICE.
1904.

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[Continued on page 3 of cover.]

A PERENNIAL RUST.

(ÆCIDIUM TUBERCULATUM E. & K. ON CALLIRRHOE INVOLUCRATA GR.)

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BUREAU OF PLANT INDUSTRY.

B. T. Galloway, *Chief.*
J. E. Rockwell, *Editor.*

VEGETABLE PATHOLOGICAL AND PHYSIOLOGICAL INVESTIGATIONS.

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[a] Detailed to the Bureau of Forestry.
[b] Detailed to Botanical Investigations and Experiments.

LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., April 20, 1904.

Sir: I have the honor to transmit herewith the manuscript of a technical paper entitled "Investigations of Rusts," by Mark Alfred Carleton, Cerealist in Charge of Cereal Investigations, Vegetable Pathological and Physiological Investigations, and recommend its publication as Bulletin No. 63 of the series of this Bureau.

The two illustrations accompanying the manuscript are necessary to a complete understanding of the subject-matter of this paper.

Respectfully,

B. T. Galloway,
Chief of Bureau.

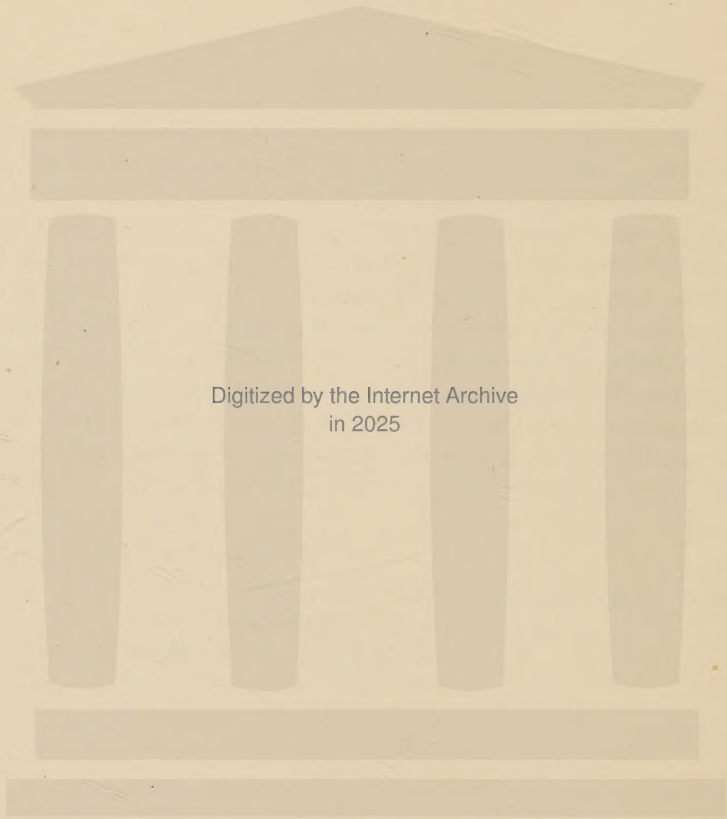
Hon. James Wilson,
Secretary of Agriculture.

PREFACE.

The experiments and observations on rusts which are the basis of the following notes were begun by Mr. Carleton several years ago, and were continued at intervals until the spring of 1900, when the pressure of other duties prevented further work of this kind up to the present time. The results obtained in many instances are still incomplete, but are of sufficient value to be recorded. Some of the species studied are of much economic importance. The investigation is a continuation of the work reported in Bulletin 16 of the Division of Vegetable Physiology and Pathology, and is concerned chiefly with the segregation of rust forms of economic importance on the common grasses and the completion of the life history of certain species. The work is to be carried on more extensively during 1904.

A. F. Woods,
Pathologist and Physiologist.

Office of Vegetable Pathological and
Physiological Investigations,
Washington, D. C., March 26, 1904.



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INVESTIGATIONS OF RUSTS.

ADDITIONS TO OUR KNOWLEDGE OF LIFE HISTORIES.

In many instances, without any experimental proof, it is inferred that there is a connection between the different forms of rust occurring on the same host plant simply because of their constant association with each other. Sometimes it is afterwards demonstrated that these inferences are wrong, though they are probably correct in a majority of cases. Studies of the following species were made with the view of obtaining a more accurate knowledge of their life history.

Euphorbia Rust (*Uromyces euphorbiæ* C. and P.).

Until the experiments herein described were performed it had not been demonstrated that there is any connection between the æcidial and other stages of this species, although experience naturally leads one to think that there is. They are in very close association on the same plant, the æcidium appearing first, quickly followed by the uredospores. In the spring of 1893 Mr. J. B. S. Norton, now professor of botany at the Maryland Agricultural College, while engaged in experiments in the germination of weeds in the greenhouses of the Agricultural Experiment Station at Manhattan, Kans., called the writer's attention to a very young rusted seedling of *Euphorbia dentata*. In this instance, as is usually the case with the young plants of this host, the pods were first badly affected by æcidia. This fact, taken together with the common observation that the seed pods of this host are usually affected by all stages of the rust, led at once to the thought that it was a case of rust propagation through the medium of the germinating seed of the host, something not before demonstrated for any other species in the entire group of Uredineæ, so far as the writer knows, unless we except the single instance of the experiments of Doctor Eriksson[a] with *Puccinia glumarum*.[b] The seed used by Mr.

[a] Vie latente et plasmatique de certaines Urédinées. Compt. Rend., 1897, pp. 475–477.

[b] T. S. Ralph, in Victorian Naturalist, Vol. VII, p. 18, describes an instance of a rust attacking the seed of *Senecio vulgaris*, stating that "with the microscope we are able to trace the fine yellow sporular matter into the covering of the seed, and into the seed itself;" but apparently it was not determined by further investigation whether or not the rust was able to reproduce itself through the germinating seed.

Norton was examined and the pods were found to be badly affected. Moreover, he stated that the seeds were planted without shelling. But the writer did not know then, as he does now, that this fact would probably make little difference, since the naked seeds are commonly affected, often showing actual peridia.

To test the theory of rust propagation above mentioned, experiments were instituted on April 22 for growing plants from rusted seed under a bell jar. The seed used bore all stages of the rust. The experiments were in five series: (1) Seeds shelled and disinfected by mercuric chlorid; (2) seeds unshelled and disinfected; (3) seeds shelled, but not disinfected; (4) seeds unshelled, not disinfected; (5) like series No. 4, but rusted mainly with æcidium. All were planted in pots in a greenhouse and the pots were kept under bell jars. On May 1 the plants began to come up. After about three months, when the plants had grown to a height of 3 to 5 inches, no rust had appeared on series 1 and 2, and only one spot on one plant of series 3. The plants of series 4 and 5 were much rusted, the æcidium appearing first, followed shortly by uredosori.

On April 25, 1893, it was attempted to germinate teleutospores of rust from the seeds used in these experiments, in water-drop cultures, which resulted in failure. On June 28, 1893, a similar culture of the fresh uredospores failed to germinate in two days.

In 1895 rusted seeds of *Euphorbia dentata*, sent from Kansas, were planted in the greenhouse of the Department of Agriculture, at Washington, D. C. From these three plants grew, which were kept under a bell jar. Soon one of these plants rusted badly, first with the æcidium, then a slight amount of the uredospores, and later the teleutospores. It should be remarked here that Euphorbia rust, so far as reported, occurs only on *E. maculata* in the vicinity of Washington, D. C., and the writer has never yet been able to obtain rusted seeds in that region.

On December 11, 1896, a third series of experiments was started at Washington, D. C. On that date rusted seeds of *Euphorbia dentata* from Kingman and Manhattan, Kans., were planted and kept under a bell jar as before. Eleven plants resulted by December 26. On March 8, 1897, spermogonia appeared in considerable amount on the young leaves of one plant, with a tendency to form a sort of hexenbesen.

On March 29 two more plants were rusted, one with spermogonia only on the young leaves, and the other with æcidia on the fruit. On April 10 still another plant showed spermogonia, making four in all, out of the eleven, that became rusted. (See Pl. II, fig. 1.)

As above stated, the proof that the rust actually penetrates the hulled seed is readily obtained, not only from microscopical demonstration, but also from the fact that the actual peridia may often be seen with the unaided eye in the seed. These experiments, however, further

demonstrate the ability of the rust to propagate itself through the medium of the germinating seed of the host, and also make it seem probable that this is even the common method of reproduction in the case of its occurrence on *Euphorbia dentata*.

It will be noted also that the results of these experiments make it almost certain that the Æcidium and Uromyces appearing upon the plants are one and the same species, since in every case all stages resulted from planting the rusted seeds, the æcidium appearing first, then the uredo, and then the teleutospores. If anything was lacking, however, the proof has since been made complete by the experiments of Dr. J. C. Arthur, as reported in the Botanical Gazette,[a] in which the uredospores and teleutospores were obtained on *Euphorbia nutans* from a sowing of æcidiospores from other plants of the same host on June 20, 1899.

As is well known, the Euphorbia rust is widely distributed over the United States, occurring on numerous host species, but it is probably most abundant on *E. dentata* and *E. preslii*. It is a significant fact, bearing upon the ontogeny of the species, that it is also on these two hosts, particularly on *E. dentata*, that the æcidium is most common, and that the rust attacks the seed so severely. The seed pods are also affected considerably in the cases of *E. lata* and *E. marginata*.

On June 12, 1897, æcidiospores of this rust had germinated very well in water-drop culture after three days, and on June 22, after a two days' culture in water of both the æcidium and uredo from *Euphorbia marginata*, the latter germinated sparingly, but the former not at all. In no instance could the teleutospores be germinated, though germination was not attempted very often.

The writer has collected all three stages of this rust on *Euphorbia maculata*, *E. marginata*, *E. dentata*, *E. preslii*, *E. glyptosperma*, and *E. heterophylla*. On *E. petaloidea* and *E. serpyllifolia* only the uredo and teleuto stages were found, and on *E. lata* and what was probably *E. geyeri* even the uredo was rarely seen.

Sunflower Rust (*Puccinia helianthi* Schw.).

Although Saccardo rightly regards this species of Schweinitz as quite distinct, and includes with it the Æcidium often associated on the same host, in many herbaria the authority of Winter and Burrill is followed in making it a form of *Puccinia tanaceti*, while the Æcidium is commonly referred to *Æcidium compositarum*, a convenient dumping ground for numerous uncertain forms. The writer has always considered this disposition of the species to be without any good reason even on a purely morphological basis, and now the experiments

[a] Arthur, J. C., "Cultures of Uredineæ in 1899," Bot. Gaz., Vol. XXIX, No. 4, pp. 270–271, April, 1900.

here recorded make it rather certain that Schweinitz and Saccardo are correct. So far as this country is concerned, the writer is convinced that *P. tanaceti* either belongs almost entirely to *tanacetum* or does not exist at all. So far it has been utterly impossible, even in a greenhouse, to make transfers of the uredo from one to another of the numerous supposed hosts of that species, except among hosts of the same genus.[a] It is, at any rate, pretty certain that the forms occurring on Vernonia, Helianthus, Actinella, and Aplopappus, which have been referred to *P. tanaceti* at various times, should be considered distinct.

The circumstances connected with the culture experiments with this species were in themselves peculiar. Late in the autumn of 1897 at Manhattan, Kans., it was desired to obtain fresh material of the uredo for inoculating various hosts, but at that date very little else than the teleuto stage could be found. Finally, on October 29 a small amount was found on *Helianthus petiolaris*, mixed among a much larger quantity of teleutospores, and from this material sowings were made on *H. petiolaris* and *H. annuus*. On November 8 there resulted one rust spot on the latter host and three on the former. The spots were of the uredo stage, but the interesting feature accompanying this culture was the appearance first of spermogonia in one of the spots. This fact made it probable that a part of the infection resulted from the teleutospores of the inoculating material, even at this unusual season for the germination of these spores. On March 7, 1898, while stationed at the University of Nebraska, inoculations of *H. petiolaris* were again made with the teleutospores only from other plants of the same host, from which numerous spermogonia appeared in eight days, followed shortly by æcidia, which were fully developed by November 1. By these results the connection of the different stages of the rust is pretty well established. At the same time it is shown that the forms on *H. petiolaris* and *H. annuus* are identical. In all cultures made of this rust both the uredospores and teleutospores have been found to germinate easily and produce infections readily. Reverse cultures with æcidiospores were not made.

These experiments were first reported at the 1900 meeting of the Society for Plant Morphology and Physiology, at Baltimore. Since that time Drs. J. C. Arthur[b] and W. A. Kellerman[c] have made a number of such experiments, confirming these results, but also seeming to indicate a distinction of host forms on different species of sun-

[a] Dr. M. Voronin at first also obtained negative results in similar experiments in Russia in attempting transfers of the rust on to other hosts. (See Bot. Zeitung, vol. 30, pp. 694–698, Sept. 27, 1872.) Later he obtained infections of *Puccinia tanaceti* from *Tanacetum vulgare* on sunflower, which, however, did not produce such vigorous growth as ordinarily. (Bot. Zeitung, vol. 33, pp. 340, 341, May 14, 1875.)

[b] Botanical Gazette, vol. 35, p. 17, January, 1903; Journal of Mycology, vol. 10, pp. 12–13, January, 1904.

[c] Journal of Mycology, vol. 9, pp. 230–232, December, 1903.

flower. Doctor Voronin, in his experiments above mentioned, also found that rust of cultivated sunflower would not infect *Helianthus tuberosus*. In 1901 Ernst Jacky[a] inoculated the following hosts with teleutospores from *Helianthus annuus*: *H. annuus*, *H. cucumerifolius*, *H. californicus*, *H. tuberosus*, *H. maximiliana*, *H. multiflorus*, *H. scaberimus*, and *H. rigidus*, with resulting infections of the three first-named species, but no infection of any of the others.

The evidence from all these experiments just quoted and those of the writer shows at least that the rusts of *Helianthus annuus* (including cultivated varieties), *H. petiolaris*, and *H. mollis* are identical, with the probability that a distinct form exists on *H. tuberosus*.

Sunflower rust has been collected by the writer on the following species of Helianthus, including all stages on nearly every species: *H. annuus* (both wild and cultivated), *H. rigidus*, *H. petiolaris*, *H. tuberosus*, *H. hirsutus*, *H. maximiliana*, *H. grosse-serratus*, *H. orgyalis*, *H. mollis*, and *H. ciliaris*. The æcidium occurs rarely in comparison with the occurrence of other stages, but is to be found on a number of hosts and occasionally in considerable abundance. This rarity of its occurrence, together with the occurrence of spermogonia so often with the uredo, may be accounted for by the fact that the uredo is often produced by direct teleutosporic infection.

Crown Rust of Oats (*Puccinia rhamni* [Pers.] Wettst.).

In a mere note in a previous bulletin of this Department[b] it is stated that certain infections had just been made showing the connection of the crown rust of oats on *Phalaris caroliniana* and *Arrhenatherum elatius* with the æcidial form on *Rhamnus lanceolata*. No other demonstration of such a connection of forms had been reported up to that time. During the same season, however, Doctor Arthur obtained infections with the æcidium of *Rhamnus lanceolata* on oats at Lafayette, Ind.[c] The experiments of the writer are here given in detail.

On August 23, 1897, the uredo stage of a rust, supposed to be *Puccinia coronata*, was found in great abundance on *Phalaris caroliniana* at Stillwater, Okla. This host, with the rust, was transferred to a greenhouse of the Agricultural College at Manhattan, Kans., and inoculations were made on oats, wheat, and orchard grass on August 30, 1897, resulting September 7 in a good infection of oats, a poor one of the orchard grass, and no infection at all of wheat. Other inoculations were made September 1 on wheat and rye, with no result. By October 8 the teleutospores had appeared on the original plants of Phalaris

[a] Centralb. Bakt. Parasit. u. Infekt., 2 Abt., Bd. 9, No. 21, pp. 802–804, December, 1902.

[b] Cereal Rusts of the United States, Bul. No. 16, Div. of Veg. Phys. and Path., U. S. Dept. of Agriculture, 1899.

[c] Bul. Lab. Nat. Hist. State Univ. Iowa, Vol. IV, pp. 398–400, December, 1898.

at Stillwater and were of the crown rust type. After this date the experiments were continued at the State University laboratories at Lincoln, Nebr., all host plants then in use being transferred to that place. On November 16 the crown rust was found, in the uredo stage, on *Arrhenatherum elatius* on the State University farm, and a rusted plant was transferred to the greenhouse. On December 11 inoculations with the rust were made on oats and rye, resulting in a good infection of the former in twelve days, but with no result on the latter. Further inoculations of oats with the Phalaris rust on February 16, 1898, resulted again in a good infection in 9 days.

No species of Rhamnus is native near Lincoln, Nebr., but *Rhamnus lanceolata* is rather common at Weeping Water, about 20 miles east of Lincoln, where it is often badly rusted with Æcidium. From that place a large amount of the Æcidium was obtained fresh on June 1, 1898. A water-drop culture of the material, made the next day, gave a profuse germination of the spores in twenty-two hours. Inoculations with the æcidiospores on oats and *Phalaris caroliniana* were made June 1 and June 2, resulting in a successful infection of Phalaris on June 14 and of oats on June 18. The oat inoculations were made simply on detached portions of the plant preserved with their broken ends in water in a damp chamber. As in all other instances, these inoculations were made with the greatest of care to prevent accidental infections. The whole series of experiments proves (1) the connection of the æcidial form of Rhamnus with the crown rust of oats, and (2) the identity of the latter with the forms on *Phalaris caroliniana* and *Arrhenatherum elatius*, besides making it probable that orchard grass may also support this species.

SEGREGATION OF HOST PLANTS.

The most important economic results of the study of rusts are likely to be derived from the investigation of the relationship of the forms on our common grasses. Such work has already been carried on to some extent by the writer and partially reported in the bulletin entitled "Cereal Rusts of the United States." A more detailed account of some of this work will be given here. Because bearing upon the same question, it seems proper to mention also some experiments with the rusts of Salix and Populus. Probably the greatest confusion exists concerning the identity of the different forms on Agropyron and Elymus, though there is much uncertainty also about those occurring on Bromus and other genera.

The experiments here described were conducted at Stillwater, Okla., Manhattan, Kans., Lincoln, Nebr., and Washington, D. C., the host plants being sometimes transferred from one place to another. Of all these rusts the one receiving most attention was the black stem rust of Agropyron and Elymus.

Black Stem Rust of Agropyron and Elymus.

At least three and probably four different rusts occur on the species of these two grass genera, and are often so closely associated that their accurate identification is extremely difficult. Of the herbarium specimens of these rusts throughout the country, probably not one in fifty is identified with any certainty. The writer's experiments with these forms are still incomplete, but a few things at least have been established. When these grasses are brought under cultivation the changed conditions and proximity to other grasses and grains cause them to become much more rusted than is ordinarily the case. In the cultivated grass plats at the experiment stations in Oklahoma, Kansas, and Nebraska the rusts were found in great abundance. It was therefore easy to carry on many culture experiments. These experiments with the uredospores of black stem rust were sufficiently numerous to make it desirable to arrange them in the following table:

TABLE I.—*Culture experiments with black stem rust of Agropyron and Elymus.*

Date.	Locality.	Origin of inoculating material.	Plant inoculated.	Period of incubation in days.	Result.
Jan. 9, 1897	Washington, D. C.	Wheat	*Elymus virginicus*	10	Success.
Do	do	do	Wheat	10	Do.
Jan. 22, 1897	do	do	*Elymus virginicus*	11	Do.
Do	do	do	*Agropyron richardsoni.*	11	Do.
Do	do	do	Wheat	11	Do.
Do	do	do	*Agropyron occidentale*	11	Failure.
Sept. 13, 1897	Stillwater, Okla	*Agropyron tenerum*	Wheat	6	Success, *a*
Do	do	do	*Agropyron tenerum*	6	Do.
Oct. 5, 1897	Manhattan, Kans.	*Agropyron occidentale*	Wheat	12	Failure.
Do	do	Wheat (originally *Agropyron tenerum*).	do	8	Success.
Do	do	do	Barley	8	(*b*)
Do	do	do	*Agropyron tenerum*	8	Failure, *c*
Oct. 21, 1897	do	do	Wheat	16	Success.
Do	do	do	Barley	16	Do.
Do	do	do	Oats	16	(*d*)
Do	do	do	Rye	16	Failure.
Do	do	*Agropyron occidentale*	Wheat	18	Do.
Do	do	do	Rye	18	Do.
Do	do	do	Barley	18	Do.
Do	do	do	*Agropyron tenerum*	18	Do.
Nov. 24, 1897	Lincoln, Nebr	do	*Agropyron occidentale*	15	Success.
Jan. 5, 1898	do	*Elymus canadensis glaucifolius.*	Wheat	21	Do. *e*
Do	do	do	Barley	21	Do.
Jan. 21, 1898	do	Wheat (originally *Elymus canadensis glaucifolius*).	Wheat	10	Do.
Do	do	do	Barley	10	Do.
Feb. 11, 1898	do	*Elymus canadensis glaucifolius.*	Wheat	14	Do. *f*
Do	do	do	Barley	14	Do.
Do	do	do	Rye	14	Failure.
Do	do	do	Oats	14	Do.
Do	do	do	*Elymus canadensis glaucifolius.*	14	Success.
Do	do	do	*Elymus virginicus*	14	Failure.
Do	do	do	*Elymus virginicus muticus.*	14	Do.
Do	do	do	*Elymus intermedius*	14	Do.
Do	do	do	*Agropyron tenerum*	14	Do.
Do	do	do	*Agropyron occidentale.*	14	Do.

a Pustules differ in color from the original.
b 1 pustule only.
c Conditions very unfavorable, however.
d Apparently 1 pustule formed.
e Rust changes color and form of pustule.
f Rust changes color.

TABLE I.—*Culture experiments with black stem rust of Agropyron and Elymus*—Continued.

Date.	Locality.	Origin of inoculating material.	Plant inoculation.	Period of incubation in days.	Result.
Feb. 11, 1898	Lincoln, Nebr	*Elymus virginicus*	*Elymus virginicus*	13	Success.
Do	do	do	*Elymus virginicus muticus.*	13	Do.
Do	do	do	*Elymus canadensis glaucifolius.*	13	Do.
Do	do	do	*Agropyron tenerum*	13	Do.
Do	do	do	*Agropyron occidentale.*	13	Failure.
Do	do	do	Rye	13	Do.
Do	do	do	Wheat	13	Do.
Feb. 21, 1898	do	Wheat (originally *Elymus canadensis glaucifolius*).	*Elymus canadensis*	7	Success.[a]
Feb. 25, 1898	do	do	*Hordeum jubatum*	11	Do.
Feb. 28, 1898	do	*Elymus canadensis glaucifolius.*	Wheat	9	Do.[b]

[a] Pustules differ in color from the original.

[b] Rust changes in appearance.

The results of these experiments, considered in connection with those recorded in Bulletin No. 16, Division of Vegetable Physiology and Pathology, U. S. Department of Agriculture, appear to establish two things, viz, (1) that the forms of black stem rust on wheat, barley, *Hordeum jubatum*, *Agropyron tenerum*, *A. richardsoni*, *Elymus canadensis*, and *E. canadensis glaucifolius* are identical, with the probability that those on *Elymus virginicus*, *E. virginicus muticus*, and *Holcus lanatus*[a] should be included; (2) that the black stem rust of *Agropyron occidentale*[b] is physiologically distinct from any other.[c]

A very interesting phenomenon in these experiments was the change in color and form of sorus of the rust produced by a transference to another host. In some cases after a transfer the rust was scarcely recognized. The change of color was sometimes from a bright yellow to a deep brown or orange, or the reverse. The uredo of *Agropyron tenerum*, for example, was often very yellow on the leaves, but changed to brown when transferred to wheat. On the species of Elymus the rust has a brown, waxy appearance, and the teleutospores long remain covered by the epidermis of the host.

[a] On January 5, 1900, quite successful infections on wheat were made with the uredospores of black stem rust of this host.

[b] Probably the most correct name of this host, which is known also as *Agropyron spicatum* and *A. glaucum* (See Hitchcock, "Note on Nomenclature," Science, vol. 17, pp. 827–828, May 22, 1903.)

[c] The form on this host was described as a distinct species, named *Puccinia agropyri*, by Ellis and Everhart, in Journal of Mycology, Vol. VII, p. 131, March 10, 1892, a fact not noticed by the writer until after most of these experiments were made. This species includes *Æcidium clematidis* D. C. according to Doctor Dietel, the proof of relationship being the result of culture experiments. (Oesterr. Bot. Zeitschr., No. 8, 1892.)

Orange Leaf Rust of Agropyron and Elymus.

In the following table are summarized the results of inoculations with the uredoform of this rust. They were carried on simultaneously with those of the black stem rust, and the material was taken chiefly from the same individual host plants.

Table II.—*Culture experiments with orange leaf rust of Agropyron and Elymus.*

Date.	Locality.	Origin of inoculating material.	Plant inoculated.	Period of incubation in days.	Result.
Dec. 21, 1896	Washington, D. C.	Rye	*Elymus americanus*	16	Failure.
Do	do	do	Rye	16	Success.
Jan. 7, 1897	do	do	*Elymus virginicus*	12	Failure.
Do	do	do	Rye	12	Success.
Feb. 1, 1897	do	do	*Elymus virginicus*	13	Failure.
Do	do	do	Rye	13	Success.
Feb. 13, 1897	do	Wheat	*Agropyron richardsoni.*	18	Failure.
Do	do	do	Wheat	18	Success.
Do	do	do	Rye	18	Failure.
Feb. 20, 1897	do	Rye	*Agropyron tenerum*	12	Do.
Do	do	do	*Triticum villosum*	12	Do.
Do	do	do	*Elymus canadensis*	12	Do.
Do	do	do	Rye	12	Success.
Mar. 30, 1897	do	do	*Agropyron caninum*	26	Failure.
Do	do	do	Rye	26	Success.
Nov. 3, 1897	Manhattan, Kans.	do	Wheat	9	Failure.
Do	do	do	Barley	9	Do.
Do	do	do	*Agropyron tenerum*	9	Do.
Do	do	do	Rye	9	Success.
Jan. 5, 1898	Lincoln, Nebr.	do	do	21	Do.
Do	do	do	*Elymus virginicus*	21	Failure.
Mar. 4, 1898	do	*Elymus virginicus*	Wheat	18	Do.
Do	do	*Elymus canadensis glaucifolius.*	do	18	Do.
Mar. 12, 1898	do	Wheat	do	14	Success.
Do	do	do	*Elymus canadensis*	14	Failure.
Do	do	do	*Elymus canadensis glaucifolius.*	14	Do.
Do	do	do	*Agropyron tenerum*	14	Do.

The chief conclusion to be derived from the results of these cultures is that the orange leaf rust is very sharply limited in its host adaptation and differs widely in this respect from the black stem rust. Similar results are given in Bulletin No. 16 of the Division of Vegetable Physiology and Pathology, U. S. Department of Agriculture, for cultures of the forms on wheat and rye. In fact, it is quite probable that almost every distinct host species bears a distinct form of the rust. One of these forms on *Elymus virginicus* L. has recently been found by Doctor Arthur to be connected with the Æcidium on *Impatiens aurea* Muhl. and is now to be known as *Puccinia impatientis* (Schw.) Arth.[a]

Black Stem Rust of Agrostis alba vulgaris.

Culture experiments with the uredoform of this rust and observations in the field indicate that it is distinct and does not occur on other

[a] Botanical Gazette, vol. 35, pp. 18–19, January, 1903.

hosts.[a] The results of the culture experiments are given in the following table:

TABLE III.—*Culture experiments with black stem rust of Agrostis alba vulgaris.*

Date.	Locality.	Origin of inoculating material.	Plant inoculated.	Period of incubation in days.	Result.
Dec. 23, 1897	Lincoln, Nebr	*Agrostis alba vulgaris.*	*Agrostis alba vulgaris.*	8	Success.
Do	do	do	Wheat	8	Failure.
Do	do	do	Oats	8	Do.
Jan. 24, 1898	do	do	Wheat	12	Do.
Do	do	do	Oats	12	Do.
Feb. 11, 1898	do	*Elymus canadensis glaucifolius.*	*Agrostis alba vulgaris.*	14	Do.

The rust is evidently of the black stem rust group (*Puccinia graminis* of authors), but contains quite a number of abnormal teleutospores, including mesospores. Many measurements of these spores average 27–54 by 16–23μ, mostly 40–46 by 16–18μ.

RUST OF CHLORIS (*Puccinia chloridis* DIET.).

The uredoform of this rust is sometimes very abundant on *Chloris verticillata* in the Great Plains region, occurring in late summer and autumn. The sori are deep brown in color. The uredospores germinate very freely and easily. In a number of experiments made in 1898 it was found that the uredo on *C. verticillata* and *C. elegans* would readily transfer from either host to the other, but not to other grasses, in several cases which were attempted. In a watch-glass culture, made March 18, 1898, of uredospores from *C. elegans*, produced from artificial infection in a greenhouse, not only these spores germinated freely, but a number of newly formed teleutospores at the same time, an occurrence unusual except in the Lepto-uredineæ. Among thousands of cultures made by the writer only one other instance of this kind has occurred. In the summer of 1895 at the Biological Laboratory at Cold Spring Harbor, Long Island, both teleutospores and uredospores taken from the same sorus of a rust on *Luzula campestris* gave good germinations.[b]

RUSTS OF WILLOW AND COTTONWOOD (MELAMPSORA).

Both the uredospores and teleutospores of the rusts of willow and cottonwood germinate readily, the germ tubes of the latter containing always brilliant endochrome. Healthy leaves of either cottonwood or willow placed in a damp chamber have often been infected by the

[a] Arthur describes culture experiments made by his assistant, William Stuart, in July, 1898, in which wheat plants were infected with uredospores from this host, but the spores of the infection sori were larger than those of the original material. (Bul. Lab. Nat. Hist. State Univ. Iowa, vol. 4, No. 4, pp. 396–397, 1898.)

[b] The species was, without much doubt, *Puccinia obscura* Schroet.

writer in nine to twelve days. The incubation period is much shortened by using germinating spores in the inoculations. In the month of October, at Manhattan, Kans., an infection was produced in this way in three days.

It was attempted by numerous inoculations with the uredoform, chiefly at Washington, D. C., to transfer the rust from willow to cottonwood and the reverse, but always without success. An interesting feature of these experiments was the discovery of the fact that the cottonwood most common in Washington, known as South Carolina poplar, could not be infected by the uredoform from the common Western cottonwood, though these two poplars are classed by some as being the same species. Moreover, the rust does not occur in nature on the South Carolina poplar, but is very abundant on the Western cottonwood, and even occurs in Washington on the few individual trees of that type growing in the city.

WINTER RESISTANCE OF THE UREDO.

In another bulletin[a] the writer has given in detail the observations and culture experiments proving the successful wintering of the uredo in the orange leaf rust of both wheat and rye. In this connection it is easy to see a number of closely correlated facts, which may mutually explain each other: (1) As shown under the preceding topic, the uredo of black stem rust may infect a number of different hosts, and therefore has a manifoldly greater chance of propagation with the same number of uredospores than if there were but one possible host; (2) as also shown, the uredo of orange leaf rust is restricted in every case to but one host, or at most to but one genus, and a much greater production of uredospores is therefore necessary for the life of the species in this stage; (3) as a corresponding matter of fact it is well known that the uredo of the latter rust exists usually in very much larger quantity than that of the former; (4) on the other hand, the teleutosporic stage is the prevailing form of the stem rust, which fact makes this rust usually the more damaging of the two, as the teleutospores infest the stem chiefly, thus more directly interfering in plant nutrition; (5) the stem rust is proved to be connected with the barberry rust, thus giving it an additional chance for increased propagation, and this through the medium of the teleuto stage instead of the uredo; (6) finally, the uredo being the prevailing form of the leaf rust, and no æcidial form being known in this country,[b] it would seem necessary that this stage of that rust should be very hardy in order to endure extremes of cold and drought and preserve the life of the species. Previous investigations of the writer and others have amply proved that this is the case. In the meantime it is found that in other species

[a] Cereal Rusts of the United States, Bul. 16, Div. Veg. Phys. and Path., U. S. Dept. of Agriculture, pp. 21–23, and 44, 45.

[b] Except in the case of the form on *Elymus virginicus* already mentioned.

there exists a similar hardiness of the uredo, of which cases the following will be discussed here:

Uredo of Kentucky Bluegrass Rust (*Puccinia poarum* Niels.).

The writer has known for some time that the uredo stage of the bluegrass rust is able to pass the winter alive and in germinating condition during any season as far north as Lincoln, Nebr., but additional evidence has been obtained from time to time. At the same time it is significant that there is no record that the teleutospores have ever been found, except in one instance, at the above-named place. In fact, few, if any, uredoforms so hardy as this one exist in this country. On February 1, 1893, this uredo was still alive in the vicinity of Manhattan, Kans. Every month of the year it exists alive and growing in great abundance everywhere about Washington, D. C. On March 2, 1898, it was found fresh on green leaves of the host at Lincoln, Nebr. On the same spot of ground it was still growing and spreading rapidly on May 8 of the same year. Host plants were transplanted that day into a greenhouse, where the rust continued to increase rapidly. As would now be supposed, the rust is sharply limited to its one host, Kentucky bluegrass. The results of the following cultures may be given in evidence.

Table IV.—*Culture experiments with the uredo of Kentucky bluegrass.*

Date.	Locality.	Origin of inoculating material.	Plant inoculated.	Period of incubation in days.	Result.
Jan. 16, 1893	Manhattan, Kans.	*Poa pratensis*	Wheat	18	Failure.
Do	do	do	Oats	18	Do.
Dec. 21, 1896	Washington, D. C.	Rye (*Uredo rubigo-vera*).	*Poa pratensis*	16	Do.
Jan. 22, 1897	do	Wheat (*Uredo graminis*).	do	11	Do.
Do	do	do	*Poa nemoralis*	11	Do.
Feb. 1, 1897	do	Rye (*Uredo rubigo-vera*).	*Poa pratensis*	13	Do.
Do	do	do	*Poa nemoralis*	13	Do.
Feb. 13, 1897	do	Wheat (*Uredo rubigo-vera*).	*Poa pratensis*	18	Do.
Feb. 25, 1897	do	*Poa pratensis*	do	10	Success.

Uredo of Puccinia montanensis Ell.

This is, in some respects, one of the most interesting of grass rusts. It is one of the "covered rusts," and is, indeed, so far covered that it is often entirely overlooked by collectors. The uredosori are very uniform in size and are exceedingly small, it being necessary often to examine them, or even find them, with a hand lens. They are elliptical in shape and placed end to end in long, narrow, yellow striæ between the veins of the leaf. The teleuto stage is so far hidden as to be detected only by a faintly darker color beneath the leaf epidermis. The rust is the most nearly like *P. glumarum* Eriks. and

Henn. yet found in this country. The known hosts are *Elymus canadensis* and *E. virginicus*, but it seems to occur on other hosts. Whether the forms on different hosts can be transferred from one to another is not yet fully determined.

The important fact now known, however, is that the uredoform is able to preserve the species over the winter without the intervention of other stages, though it is possible that extensive propagation is aided by other stages. October 28, 1897, fresh uredosori were observed on *Elymus canadensis* at Manhattan, Kans., and again in the same locality on November 2. But as early in the spring as May 26, at Lincoln Nebr., when there was yet but a small beginning of vegetation, the uredo had burst the epidermis of the host in grass plats at the University farm. Previous to this the living uredo had been observed in these plats practically every month of the winter.

In other instances the uredospores of certain species are so very abundant and the teleutospores so rare that there seems a probability that such species are carried over from summer to summer largely through the uredo stage alone, though there is no absolute proof of such a course. Two instances are particularly interesting—those of the uredos of *Puccinia cryptandri* Ell. and Barth., and *Puccinia* on *Panicum autumnale*.[a] The uredospores of these species begin to be conspicuously abundant about midsummer, but continue in considerable abundance until very late in autumn. The uredo of *Panicum autumnale* was found in germinating condition in Kansas up to November 3 in 1897. A water-drop culture of uredospores of this species gave excellent germination in ten hours August 21, 1897, at Perkins, Okla. The uredospores of *Puccinia cryptandri* were found in extreme abundance in Oklahoma until October 11, 1897, but in all cases without any accompanying teleutospores. Often the uredosori had a fresh appearance on portions of leaves that were quite dead.

EMERGENCY ADAPTATIONS.

In connection with some culture experiments conducted at Lincoln, Nebr., in the botanical laboratory of the State University, in February, 1898, a water-drop culture was made (February 3) of uredospores of the above-mentioned *Puccinia cryptandri* which had been collected on October 8, 1897, at Perkins, Okla., and kept to date as herbarium specimens. A fair germination resulted in twenty-four hours. Spores from the same collection were used on February 16 to inoculate seedlings of *Sporobolus airoides*,[b] with the result of the appearance of two rust spots by March 16. These spots may really have appeared much earlier and been overlooked, as they were very small and the host

[a] Perhaps a new species, needing further study.

[b] Apparently this same species of rust had already been collected on *Sporobolus airoides* in the same locality where the collection from *S. cryptandri* was made.

itself is well known to have extremely narrow leaves. Moreover, the spores were not germinated when applied, and, being from dried specimens, the incubation period would naturally be long. Seedlings of *S. cryptandri* were not at the time available. On March 16 a second water-drop culture was made from this dried material, resulting in the germination of a few spores.

Teleutospores from herbarium specimens have often been germinated, but the writer knows of no other instance of the germination of dried uredospores, such spores being able also to infect a different host. These observations and experiments indicate that we have here a second step in the perfection of the uredo stage as a means of propagating the species. The first step, the attainment of sufficien hardiness to continue alive in the green plant over winter, has just been discussed. Even in this case the uredo, although quite active, at least displaces the resting spore, and in a measure performs its part. But as the perennial host becomes more like an annual and the plant dies nearly or quite to the ground, as in this particular case of the Sporobolus (which is quite different in this respect from the evergreen *Poa pratensis*, for example), necessarily, in the absence of teleutospores, the uredospore must be able to infect after a dormant period. The uredospore therefore becomes now practically a resting spore, but retains the appearance and manner of germination of the summer spore. Such a modification in form or function of any stage of a species to correspond with an unusual change of condition of climate or of the host may be considered as an *emergency adaptation*.

It is easily understood how the change of conditions may be so severe as to necessitate still further modification of structure as well as function, simply as a means of protection. Such a development seems to have been actually reached in the species next discussed, which has resulted in the production of a distinct spore form, specialized from the uredo, leaving still, however, a true uredo stage for summer propagation.

Puccinia vexans Farl.

There are probably no other species in all the Uredineæ more interesting than this one, and certainly none that has been more perplexing. In this species there are three distinct spore forms aside from any æcidium or spermogonium that may possibly exist true uredo and teleuto stages, and a peculiar one-celled form different from either of these. (Pl. II, figs. 2–9.) The species was at first made all the more puzzling by the rarity of the true uredo stage, which was not known to exist, or at least not reported, until 1890, when Dr. H. J. Webber, in the Catalogue of the Flora of Nebraska, reported its occurrence in that State. In certain seasons and localities the teleuto stage also is almost or entirely lacking.

The species was first described by Peck as a Uromyces (*U. brandegei* Pk.)[a] on the basis of material collected by Mr. T. S. Brandege, in which specimens contained only the third spore form. Because of the discovery afterwards of two-celled spores associated with this third spore form, even sometimes in the same sorus, Doctor Farlow described it as a Puccinia (*P. vexans* Farl.) in the Proceedings of the American Academy of Arts and Sciences, Vol. XVIII, pp. 82–83. At that time the true uredo stage had not been discovered.

This third spore form is far more prevalent than either of the others as a rule, but is sometimes entirely absent, leaving only the teleuto stage. It is distinct from either of the other forms in structure and appearance, and yet resembles both in some respects. It is larger than either of them, is strongly papillate, and has a much thicker cell wall, but on the other hand possesses the color and persistence of pedicels of teleutospores and appears to have pores like the uredospores. (Pl. II, fig. 5.) Doctor Farlow, in his description, says:

> A species in which some of the sori contain only two-celled spores must certainly be held to be a Puccinia, and the perplexing question arises, are the one-celled spores a unilocular form of teleutospores similar to what is known in *P. cesatii* Schr., or are they the uredospores of this species? I have not been able to find any other spores which represent the uredo of the species; and never having seen the unicellular spores in germination, there is, so far as we yet know, no reason why they may not be the uredospores. On the other hand, their general appearance and the density of the cell wall would lead one to suppose that they were of a teleutosporic nature. Further conjecture is unnecessary, because, as the species is not at all rare in some localities, botanists who can examine the fungus on the spot ought to be able to ascertain whether the one-celled bodies produce promycelia or not, or else to discover the true uredo of the species.

A full description of all three forms is given by Arthur and Holway in Descriptions of American Uredineæ accompanying Fasicle IV of Uredineæ Exsiccatæ et Icones.[b]

After numerous unsuccessful trials during several years, the writer was finally able to germinate the third spore form, and, as suggested by Doctor Farlow, has in this way been able to determine its nature. In manner of germination it is exactly like the uredospore, the long simple germ tubes being produced through equatorial pores (Pl. II, figs 7 and 8), but is like the teleutospore in germinating only after a dormant period and exposure to extremes of weather. The uredo and teleuto forms being already present and morphologically different from this form, it must be considered distinct. Because of the dual nature of this spore form, the writer has already proposed for it the name *amphispore* in a paper read before the Baltimore meeting of the Society for Plant Morphology and Physiology in 1900, only an abstract of which was published.[c] The term has since been adopted by Arthur

[a] Bot. Gaz., 4: 127.

[b] Bul. Lab. Nat. Hist. State Univ. Iowa, Vol. V, pp. 329–330.

[c] Science, Vol. XIII, p. 250.

approach other groups, and, indeed, after further experiment, may have to be placed in some other group. The following species have given interesting results in culture experiments.

Rust of Cocklebur (*Puccinia xanthii* Schw.).

Observations and culture experiments of the writer show that the rust of cocklebur is probably limited to one host and is distinct from the species on Ambrosia, and also justify the suspicion that it lies very near the border of the Lepto-uredineæ, and may belong to another group.

On March 1, 1897, the first water-drop culture made gave an excellent germination in forty-eight hours. Long promycelia were produced, but no sporidiola. On February 13, 1897, at Washington, D. C., inoculations were made on seedlings of cocklebur and *Ambrosia trifida*, resulting in an infection of the former in eighteen days, but not of the latter. On March 12 a second experiment resulted in a large number of infections of cocklebur seedlings in fourteen days. In all these cases spermogonia preceded the teleutospores in the infected spots. On October 8 of the same year an æcidium was found on cocklebur in considerable abundance, associated with the teleutosori, at Perkins, Okla. An inoculation on cocklebur seedlings, made at Lincoln, Nebr., on February 16, 1898, resulted in the production of spermogonia in ten days. The inoculating material had been collected in October, 1897. An æcidium on cocklebur was again found in abundance at Las Cruces, N. Mex., on July 11, 1899. Attempts should be made to infect the cocklebur with this æcidium. Doctor Farlow says an æcidium on Xanthium in Massachusetts is frequently followed by *Puccinia xanthii*.[a]

The ease with which artificial infections are made with this rust is at first surprising. So long as there is warmth and moisture, germination occurs under almost any condition and at any time.

Rust of Velvet Leaf (*Puccinia heterospora* B. and C.).

In the last-mentioned experiments the inoculating material was taken each time from dead leaves. The same was true in one experiment with the rust of velvet leaf, November 14, 1896, at Manhattan, Kans., in which seedlings of the host were infected in twelve days. For all these experiments the average time of incubation was about twelve days. In December, 1896, the infected plants of the last experiment were transferred from Manhattan to Washington, D. C., and material from these was used to inoculate new seedlings, which resulted in an infection in nine days. It appears, therefore, that the

[a] Proc. Amer. Acad. Arts and Sci., Vol. XVIII, p. 75.

incubation period is shorter if inoculating material is taken from living plants, and during the summer it is probably about the same as that of infections from uredospores.

Numerous experiments were also made with other lepto species, including *Puccinia grindeliæ*, Pk., *P. variolans*, Hark., *P. lygodesmiæ*, E. and E., and *P. sharpiana*, Körn, with results similar to those above mentioned. The writer has already called attention to the phenomenon of the formation of catenulate sporidiola in two of these species, *P. grindeliæ* and *P. variolans*.[a]

PERENNIAL SPECIES.

The chance for the continued existence of a rust through winter resistance of the uredo without the intervention of another stage has been discussed. Though such a condition can only exist on a perennial host, or at least one that lives over winter, it must not be supposed that the fungus itself is necessarily or even usually perennial. As fast as the leaves of the host die the spores simply drop on to the next lower and younger leaves and produce reinfection, the mycelium not extending through the base of the infected leaf into the next leaves. If, however, the mycelium is found within the rootstock and after a dormant period during midwinter follows the new shoots upward in early spring and again produces sori at the surface of the plant, the rust is a true perennial. This condition appears to exist in the following species.

Æcidium tuberculatum E. and K.

It is now usually supposed that all æcidial forms will likely be found to be connected with other stages, though there are probably more of these forms whose connections are at present undetermined than there are of Lepto-uredineæ. If any Æcidium is more likely than another to be an independent species, certainly the probabilities are largely in favor of this species, which occurs on *Callirrhoe involucrata*,[b] for there is no need of another stage to perpetuate it, though another host might give it a wider distribution.

The striking orange-yellow color, large and otherwise conspicuous sori, and its complete attack of every portion of the host make this an unusually unique and attractive species (Pl. I, frontispiece). A note concerning the hardiness of this species was published by the writer several years ago.[c] The words are here quoted: "*Æcidium tuberculatum*

[a] Bot. Gaz., Vol. XVIII, pp. 455–456.

[b] Though not previously reported, this rust was found also on *Callirrhoe alceoides* at Salina, Kans., in May, 1893.

[c] Bot. Gaz., Vol. XVIII, p. 453.

E. and K. is still producing æcidiospores on *Callirrhoe involucrata* outdoors here at Manhattan at the time of this writing (October 15, 1893), and Mr. E. Bartholomew, of Rooks County, Kans., tells me that he has seen in December æcidiospores on specimens of this host growing close by a large snowdrift. In the spring æcidiospores of this species begin forming about the first day of April." On December 20, 1893, after the above was transmitted for publication, the rust was found still alive although it had been under 4 inches of snow. In a water-drop culture of some of the material four spores germinated in twenty-four hours. Since that time, at later dates in the winter the living rust has been found, but close within the rootstock, with a faint color still, but producing no spores. The peculiar manner of growth of the rust, permeating the entire host and producing scattering sori all along the stems to their bases, as well as on the leaves, and the difficulty of germinating the spores harmonize also with the idea of a propagation by perennial mycelium. Besides the above instance other cultures of the spores were made as follows: At Manhattan, Kans., May 20, 1893, spores from *Callirrhoe alcæoides*, only a few germinations in forty-eight hours; at Manhattan, June 9, 1893, spores from *C. involucrata* germinated sparingly in twenty-five hours; at Manhattan, January 30, 1894, spores from *C. involucrata* growing in greenhouse, fair germination in sixty hours.

In the winter of 1896–97 infected plants of *C. involucrata* were obtained from Kansas and grown in a greenhouse at Washington, D. C., and on March 17, 1897, inoculations of seedlings of the following grasses with spores from these plants failed to produce infections: *Agropyron occidentale*, *A. richardsoni*, *Sitanion elymoides*, *Elymus canadensis*, and *Bouteloua racemosa*.

Rust of Peucedanum Fœniculaceum.

An Æcidium occurs on this host in Kansas and Nebraska which has been reported as *Æ. anisotomes* Reich., but the identity of which is not yet determined[a] satisfactorily to the writer. At certain places a Puccinia follows the Æcidium so closely that their connection is very probable. Both forms are particularly abundant at Manhattan, Kans. On April 25, 1893, at that place, it was determined by the study of many cross sections of the host plant that the mycelium of the Æcidium extends into the rootstock. It is one of the earliest rusts in the spring to appear in that locality. These facts make it probable that this rust is also perennial. On the other hand, it is possible that the teleutospores of the Puccinia may produce a very early infection at the base of the young shoots, resulting in the Æcidium, although in some localities no Puccinia has yet been found following the Æcidium.

[a] The species is probably *Puccinia jonesii* Pk., with the æcidial stage present.

At Lincoln, Nebr., on March 24, 1898, teleutospores of this same Puccinia germinated in a water-drop culture in twenty-four hours.

It should be noted that it is possible for a perennial rust to exist in an annual host, the mycelium of the rust being carried over winter in the seed of the host. Such an instance is practically certain in the Euphorbia rust already discussed. Granting that Doctor Eriksson's experiments were accurate, there would be another example in *Puccinia glumarum* Eriks. and Henn. on wheat.

PLATES.

DESCRIPTION OF PLATES.

PLATE I. *Frontispiece.* A perennial rust. *Æcidium tuberculatum* E. and K. on *Callirrhoe involucrata* Gr.

PLATE II. Fig. 1.—Seedling of *Euphorbia dentata* grown constantly under bell jar from rusted seed. Fig. 2.—*Puccinia vexans* Farl. on *Bouteloua racemosa*, both uredosori and amphisori being shown. (Natural size.) Fig. 3.—The same uredosori and amphisori shown in fig. 2 magnified 10 diameters. Fig. 4.—Uredospores of *Puccinia vexans* × 600. Fig. 5.—Amphispores of *Puccinia vexans* × 600. Fig. 6.—Teleutospore of *Puccinia vexans* × 600. Fig. 7.—Germinating uredospore of *Puccinia vexans* × 300. Fig. 8.—Germinating amphispores of *Puccinia vexans* × 300. Fig. 9.—Uredosori of *Puccinia vexans* on young seedling leaf of *Bouteloua racemosa* produced by artificial infection with uredospores from the same host. (Natural size).

RUSTS OF EUPHORBIA AND GRAMA GRASS.

[Continued from page 2 of cover.]

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